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Shore Disturbance and Dune Plant Distribution

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ABSTRACT

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Topographic and edaphic characteristics and the floristic composition were determined along five strip-transects in ten dune areas along the southern Brazilian coast, each subject to different overwash frequencies and prevailing wind patterns. The relative frequency of each species was estimated in 10 m wide zones parallel to the beach. Plant association analysis was done on 17 (≥4.5% average frequency) out of the 37 species recorded. Cluster analysis characterized four vegetation associations with dominance of *Blutaparon portulacoides, Hydrocotyle bonariensis-Paspalum vaginatum, Spartina ciliata,* and *Panicum racemosum.* Discriminant analysis separated *Blutaparon, Spartina* and *Panicum* associations along a gradient of increasing seawater overwash disturbance as the principal abiotic discriminant function. Height above mean low water, beach inclination, sediment pH, and fine particle content gradients significantly correlated with the primary discriminating factor. A second abiotic function described a sand particle size gradient, which separated *Panicum* and *Hydrocotyle-Paspalum* associations, the latter being characteristic of a few sites where drainage creeks break the dunes or seasonal waterlogging occurs. The *Blutaparon* association occurs on backshores along the entire southern brazilian coast, whilst a gradient of increasing disturbance is likely to be responsible for the substitution of *Panicum* and *Spartina* foredune associations.

ADDITIONAL INDEX WORDS: *Dune plant distribution, vegetation changes, natural disturbance, Brazil.*

INTRODUCTION

Natural disturbance is a source of spatial and temporal heterogeneity for shore plant community structure and dynamics (Keddy, 1983; Sousa, 1984; Watkinson and Davy, 1985). Analogous affirmations for coastal backshore and foredune plant communities still lack the desired support. Physical disturbance, owing to natural seawater overwash events with massive sand transport and temporary inundation, decreases from both active transgressive dune fields to prograding dune systems (Hesp, 1991; Fahrig *et al.,* 1993) and from backshore to foredune plant communities (Bernardi and Seeliger, 1989; Barbour, 1992). The resulting stressful local sand burial, sand abrasion, salinity, temperature, moisture and nutrient gradients might explain variation in species number and composition between these communities (Keddy, 1985; Hesp, 1991; Barbour, 1992).

Recent studies along the southern part of the Brazilian coast have concentrated on physical (Bernardi and Seeliger, 1989; Costa *et al.,* 1991), sedimentologic (Calliari and Klein, 1993), and floristic aspects (Cordazzo and Seeliger, 1988; Costa and Seeliger, 1990; Seeliger, 1992), but no cause and effect relation between shore disturbance gradients and backshore/foredune vegetation has yet been demonstrated. Since this information is paramount for effective dune management, this study aims to identify the principal backshore and foredune plant associations and to interpret their response along a natural disturbance gradient.

STUDY AREA

Approximately 700 km of continuous coastal dunes between Cabo St. Marta (Brazil) and La Coronilla (Uruguay) are exclusively colonized by herbaceous plants. The study area was located in the southernmost 217 km long stretch (32° 10′–33° 40′ S) and represents a warm temperate transition zone (Cordazzo and Seeliger, 1988). Beaches and dunes are composed of fine quartz sand with low organic matter content and a high proportion of shell fragments (Cordazzo and Seeliger, 1987). Since the regional tidal range is less

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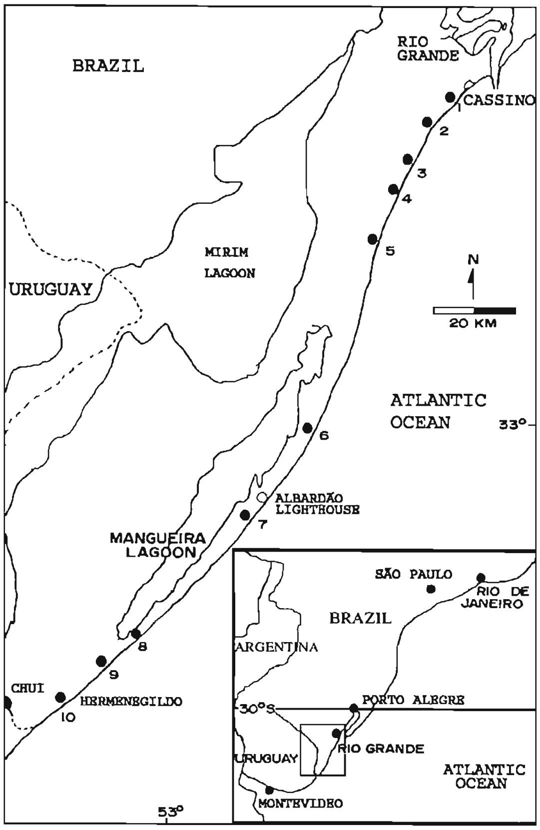

Figure 1. Region studied. Numbers on the map show the position of the areas sampled quantitatively.

than 50 cm, beach overwash is a function of storm tides (Bernardi *et al.*, 1987). In general, seasonal changes of beach and foredune profiles are a function of prevailing SE winds during winter and NE winds during summer (Costa *et al.*, 1991). However, changes between coastline orientations north and south of 33° S imply in differences between the approach angle and the impact of onshore winds. As a result, gradients in overwash frequency and sand transport induce dissipative beaches in the north and reflective beaches with coarser-textured sand in the south of the region (Calliari and Klein, 1993). Also foredune physiographies change from about 7 m high frontal dune ridges, to spaced rounded 1–2 m high hummock dunes, to large nearshore deflation plains in a north-south direction (Seeliger, 1992).

MATERIAL AND METHODS

Ten areas were selected to include all types of physiographies (Figure 1). In each area five 100 m long and one meter wide strip transects, starting at the leading edge of the vegetation, were placed at 20 m intervals perpendicular to the beach. The presence or absence of plant species was determined along each transect at 2 m intervals using 1 m^2 quadrats. In each area, the floristic data of 25 quadrats in 10 m wide zones parallel to the beach, were pooled to express percent frequency of plant species occurrence. The resulting 100 zones (10 zones in each of the 10 areas) were classified by a cluster analysis hierarchy (Romesburg, 1984).

Only species with an average frequency ≥ 4.5 % in any one of the 10 areas were considered. The Pearson correlation coefficient was calculated between all pairs of zones. Owing to the unequal represention in the data of the plant associations, and to prevent abundantly sampled plant association from having an overly large influence, the WPGMA (Weighted Pair Group Method Arithmetic) linkage clustering technique (Pielou, 1984; Romesburg, 1984), rather than the UPGMA (Unweighted Pair Group Method Arithmetic), was applied to construct the dendrogram.

To evaluate the intensity of disturbance, coastal orientation, the width and slope of the beach between mean low water (MLW) and the starting point of the strip transects and the height of each quadrat relative to MLW were determined in all areas. The particle size composition (<0.062, 0.062–0.25, 0.25–0.50, >0.50 mm) and pH of superficial sand (10–20 cm depth) were analysed at 10 m intervals along each transect in all areas. Discriminant analysis of standardized values of abiotic variables was used to test the hypothesis that the abiotic factors distinguished the plant associations obtained by cluster analysis. The discrimination between centroids were tested by Wilk's "Lambda" statistic and Rao's "V" statistic, showing the multidimensional distance between associations (Kleka, 1975).

RESULTS

A total of 37 species were recorded on backshore and foredune areas, though only 17 species (≥ 4.5% average frequency in any one of the areas) served for association analysis. *Panicum racemosum, Blutaparon portulacoides, Paspalum vaginatum, Spartina ciliata,* and *Hydrocotyle bonar-*

Table 1. *Percentage frequency of plant species on dunes of the southern Brazil coast.*

Species	Frequency per Area (%)										Frequency (%)	
	1	2	3	4	5	6	7	8	9	10	Average	Maximum
Panicum racemosum Spreng	23.2	62.0	16.3	91.2	70.7	34.6	12.3	13.2	58.5	83.3	46.5	91.2
Blutaparon portulacoides St. Hill.	84.5	44.2	54.3	41.6	12.8	26.8	42.3	26.7	32.8	12.8	37.9	84.5
Paspalum vaginatum O. Swartz	28.4	21.2	16.1	2.0	0.4	6.4	20.1	82.8	53.0	12.1	24.3	82.8
Spartina ciliata Brong.	18.9	20.7	40.3	11.1	11.0	62.2	31.0	22.6	75.1	23.8	31.7	75.1
Hydrocotyle bonariensis Lam.	4.6	16.8	3.2	6.5	3.6	6.2	15.0	66.0	58.9	48.5	22.9	66.0
Senecio crassiflorus (Poir) DC	—	—	—	1.5	7.4	—	—	4.1	20.5	31.4	6.5	31.4
Androtrichum tryginum (Pfeiffer) Spreng	12.5	8.1	1.1	7.5	1.4	2.7	—	24.6	5.9	31.1	9.5	31.1
Calycera crassifolia (Miers) Hick	—	—	—	—	—	—	—	4.8	10.4	2.0	1.7	10.4
Eleocharis nodulosa (Roth) Schult.	—	—	—	—	—	—	—	8.0	—	—	0.8	8.0
Juncus acutus L.	7.1	—	—	—	—	—	—	0.3	0.4	—	0.8	7.1
Calystegia soldanella (L.) R. Br.	—	—	—	—	—	—	—	—	0.8	6.8	0.8	6.8
Fimbristylis autumnalis (L.) Roemer et Schult	—	—	—	—	—	—	—	5.8	—	—	0.6	5.8
Scirpus cernuus Vahl.	—	—	—	—	—	—	—	5.7	0.4	—	0.6	5.7
Cakile maritima Scopoli	—	—	—	—	—	0.4	—	—	0.8	5.2	0.6	5.2
Plantago australis Lam.	—	—	—	—	—	—	—	1.0	—	4.9	0.6	4.9
Sisyrinchium sp. L	—	—	—	—	—	—	—	—	—	4.8	0.5	4.8
Cyperus reflexus Vahl.	—	—	—	—	—	—	—	—	0.7	4.5	0.5	4.5
Triglochin striata Ruiz et Pav.	—	—	—	0.3	—	—	—	3.9	0.4	—	0.5	3.9
cf. *Spilanthes* Jacq.	—	—	—	—	—	—	—	—	—	3.6	0.4	3.6
Gamochaeta americana (Mill.) Weddell	0.7	0.7	—	0.8	2.0	—	—	2.3	—	2.8	0.9	2.8
Cyperus obtusatus (Presl.) Mattfeld et Kuk.	—	—	—	0.4	—	—	—	2.7	—	—	0.3	2.7
Bacopa monnieri (L.) Pennell	—	—	—	—	—	—	—	2.3	2.7	—	0.5	2.7
Conyza floribunda Humbold, Bonpland et Kunth	1.0	0.3	—	2.0	—	—	—	1.3	2.6	2.1	0.9	2.6
Baccharis patens Baker	—	—	—	—	—	—	—	—	—	2.6	0.3	2.6
Porophyllum cf. *americanum* DC	—	—	—	—	—	—	—	—	—	2.4	0.2	2.4
Centella hirtella Nannf	—	—	—	—	—	—	—	—	—	2.2	0.2	2.2
Ischaemum minus Presl.	—	—	—	—	—	—	—	—	—	2.2	0.2	2.2
Solanum cf. *americanum*	—	—	—	—	—	—	—	—	—	1.6	0.2	1.6
Andropogon arenarius Hackel	—	—	—	—	0.4	—	—	—	—	1.5	0.2	1.5
Lindergia dubia (L.) Pennell	—	—	—	—	—	—	1.3	0.3	—	—	0.2	1.3
Indigofera sabulicola Benth	—	—	—	—	—	—	—	—	—	1.2	0.1	1.2
Polygala cyparissias St. Hil.	—	—	—	—	—	—	—	—	—	0.8	0.1	0.8
Phyla canescens Greene	—	—	—	—	—	—	—	0.7	—	—	0.1	0.7
Conyza pampeana Parodi	—	—	—	0.4	—	—	—	—	—	—	<.0.1	0.4
Vigna luteola (Jacq.) Benthan en Martius	—	—	—	—	0.4	—	—	—	—	—	<0.1	0.4
Senecio selloi (Spreng) DC	—	—	—	—	—	—	0.3	—	—	—	<0.1	0.3
Oenothera affinis Cambessedes en St. Hil.	—	0.3	—	—	—	—	—	—	—	—	<0.1	0.3

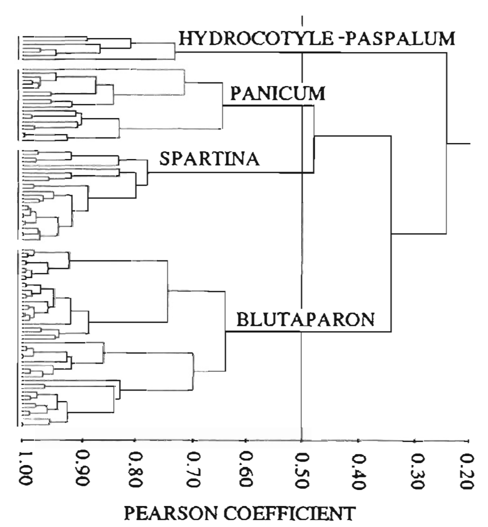

Figure 2. Cluster analysis of 100 dune zones of the southern Brazilian coast, using as attributes the percentage frequencies of the most abundant (> 4.5%) plant species.

Table 2. *Average percentage frequency of the dominant plant species in different association identified by cluster analysis of the species frequencies.*

	Associations			
Species	1	2	3	4
Blutaparon portulacoides	65	23	7	6
Spartina ciliata	31	64	14	15
Panicum racemosum	31	48	86	10
Paspalum vaginatum	23	30	7	83
Hydrocotyle bonariensis	7	39	23	85
Androtrichum trigynum	3	5	18	35
Senecio crassiflorus	<1	11	15	6
Calycera crassifolia	1	5	<1	4
Juncus acutus	2	<1	—	<1
Cakile maritima	—	2	1	—
Sisyrichium sp	—	—	2	—
Calystegia soldanela	—	<1	3	—
Cyperus reflexus	—	<1	2	—
Plantago australis	—	—	2	2
Scirpus cernuus	—	<1	—	8
Fimbristylis autumnalis	—	—	—	8
Eleocharis nodulosa	—	—	—	11

Association 1 = *Blutaparon*; 2 = *Spartina*; 3 = *Panicum*; 4 = *Hydrocotyle-Paspalum*

iensis were dominant species with an average frequency of >20% and maximum frequencies of 66 to 99% in at least one of the areas (Table 1). Cluster analysis characterized four associations with less than 50% weighted average intergroup correlations (Figure 2). In each association the dominant species exceeded average frequencies of 64% and was always co-dominant in all other associations. The *Blutaparon* association (1) was characterized by the highest number of zones (48), but least co-occurrence of other species. The *Spartina* association (2) and the *Panicum* association (3) were characterized by the co-occurrence of *Calycera crassifolia, Cakile maritima, Senecio crassiflorus, Calystegia soldanella,* and *Cyperus reflexus,* as well as by the exclusive occurrence of *Sisyrichium sp* and *Plantago australis* in the latter. A *Hydrocotyle-Paspalum* association (4) was least frequent (7 zones) and was characterized by the co-dominant *Androtrichum trigynum* and exclusive occurrence of *Eleocharis nodulosa* and *Fimbristilis autumnalis* (Table 2).

The analysis of abiotic variables showed significant differences between associations and coordinated gradients between the abiotic variables (Table 3). The main coordinated gradient was identified by the abiotic discriminant function 1 (AF1) (Table 4). Abiotic function 1 was positively correlated to average height above MLW, which significantly correlated with shore inclination ($r=0.56$, $P< 0.01$). The AF1 discriminated both the *Blutaparon* association (1), closest to MLW, and the *Spartina* association (2) with steepest shore inclination from the other associations (see Steps 1 and 2 of Table 4). The *Panicum* (3) and *Hydrocotyle-Paspalum* (4) associations were separated by the abiotic function 2 (AF2), which described an increase in medium and a decrease in fine particles (Table 4, Steps 3 and 4). Together the discriminant functions AF1 and AF2 accounted for 78.7% of the explained variance and classified the zones with 92% accuracy. Differences in relative frequency among *Blutaparon* (1), *Hydrocotyle-Paspalum* (4), *Spartina* (2), and *Panicum* (3) associations identified abiotically distinct sites, characterized by increasing dune height, MLW distance, silt/clay fractions, and reduction of pH (Figure 3).

DISCUSSION

Component species of backshore and foredune plant associations are selected in accordance to morphologic and reproductive traits and their physiological tolerance (BARBOUR *et al.*, 1976; 1987; FAHRIG *et al.*, 1993) to local salinity, water, nutrient, and edaphic conditions, caused by shore

Table 3. *Averages (standard-errors) of the values of abiotic variables in each plant association. All Kruskal-Wallis tests were significant at P < 0.01 level.*

	Association				Kruskal-Wallis
Abiotic Variable	1	2	3	4	
MLW distance* (m)	40.80 (3.80)	65.00 (6.50)	68.00 (4.70)	77.10 (6.80)	23.1
pH	8.48 (0.05)	7.67 (0.09)	7.33 (0.18)	8.15 (0.06)	63.1
Coarse sand (%)	0.08 (0.03)	0.39 (0.14)	0.03 (0.01)	0.50 (0.23)	12.0
Medium sand (%)	2.92 (0.30)	4.49 (0.82)	2.37 (0.33)	11.04 (2.80)	16.0
Fine sand (%)	96.51 (0.32)	94.70 (0.95)	96.23 (0.43)	88.24 (2.99)	13.9
Clay and silt (%)	0.15 (0.01)	0.28 (0.06)	0.38 (0.06)	0.12 (0.04)	15.1
Average height (m)	2.41 (0.12)	4.23 (0.26)	4.38 (0.17)	3.51 (0.24)	48.8
Beach inclination (°)	1.18 (0.04)	1.77 (0.08)	1.28 (0.03)	1.14 (0.01)	36.4
NE wind angle (°)	92.50 (1.40)	98.80 (3.40)	81.30 (4.30)	100.30 (0.30)	18.0
Latitude (°)	32.67 (0.07)	33.35 (0.07)	32.85 (0.12)	33.54 (0.04)	31.2

*MLW = Mean low water
Association 1 = *Blutaparon*; 2 = *Spartina*; 3 = *Panicum*; 4 = *Hydrocotyle-Paspalum*

disturbance gradients of seawater overwash and wind-controlled sand deposition patterns (Godfrey, 1977; Costa *et al.*, 1991; Hesp, 1991). In spite of cyclic exposure to erosive seawater flooding, the *Blutaparon* association occurs on backshores along the entire coast because the plants withstand saline stress and sand instability, owing to rhizome-propagated perennial growth (Bernardi *et al.*, 1987). In contrast, unstable backshore conditions frequently disrupt the life cycle of annual species; therefore *Cakile maritima, Calystegia soldanella,* and *Calycera crassifolia,* which form a common driftline association elsewhere (Doing, 1985), retract along southern Brazilian beaches to more stable conditions. Only where drainage creeks break the dunes or where seasonal waterlogging causes occasional freshwater inundation stress, the *Blutaparon* association is replaced by a *Hydrocotyle-Paspalum* association on the backshore. As has been observed in dune systems elsewhere (Moreno-Casasola and Espejel 1986; Barbour *et al.* 1987) under these conditions, the pronounced phenotype plasticity of *Hydrocotyle bonariensis* (Costa and Seeliger, 1990) and the extensive and fast growing integrated rhizome system enable the species to compensate for nutrient limitation or local competition (Costa and Seeliger, 1988a; Evans 1988). Both, the local co-dominance (*Paspalum vaginatum, Androtrichum trigynum, Eleocharis nodulosa, Fimbristilis autumnalis*) and occasional occurrence (*Bacopa monnieri, Polygala cyparissias, Phyla canescens, Cyperus obtusatus, Cyperus reflexus, Triglochin striatum, Ischaemum urvellianum, Centella hirtella*) of humid sand indicators (Pfadenhauer, 1980; Cordazzo and Seeliger, 1988; 1993) confirms this patterns for the southern Brazilian coast.

A north-south gradient of increasing shore disturbance is likely to be responsible for the sub-

Table 4. *Abiotic discriminant analysis of the plant associations on dunes of the southern Brazilian coast. The stepwise introduction of the significant (P < 0.05) abiotic variables for discrimination into the analysis (Method of RAO), the characterization of the correlation coefficients (r) and the canonical standardized coefficients of the abiotic variables that discriminated the associations are also shown.*

			Association			
Step	Introduced Variable	Change in V	1	2	3	4
1	Average height	101.5*	A	BCD	BCD	BCD
2	Inclination	67.9*	A	B	CD	CD
3	Medium sand	62.4*	A	B	C	D
4	Clay and silt	57.2*	A	B	C	D
5	MLW distance	34.5*	A	B	C	D
6	Latitude	39.7*	A	B	C	D
7	NE wind	38.9*	A	B	C	D
8	Coarse sand	24.6*	A	B	C	D
9	Fine sand	23.4*	A	B	C	D
10	pH	19.2*	A	B	C	D

Explained Variance (%)	AF	Variable	(r)	Standardized Coefficient
52.7*	1	Avg. height	(0.60)	0.26
		pH	(−0.57)	−0.35
		Clay and silt	(0.32)	0.81
		MLW distance	(0.27)	0.60
26.0*	2	Medium sand	(0.64)	1.41
		Fine sand	(−0.57)	0.74
		Latitude	(0.37)	0.91

*Significant at P < 0.01
†Different letters show significantly (P < 0.05) different association

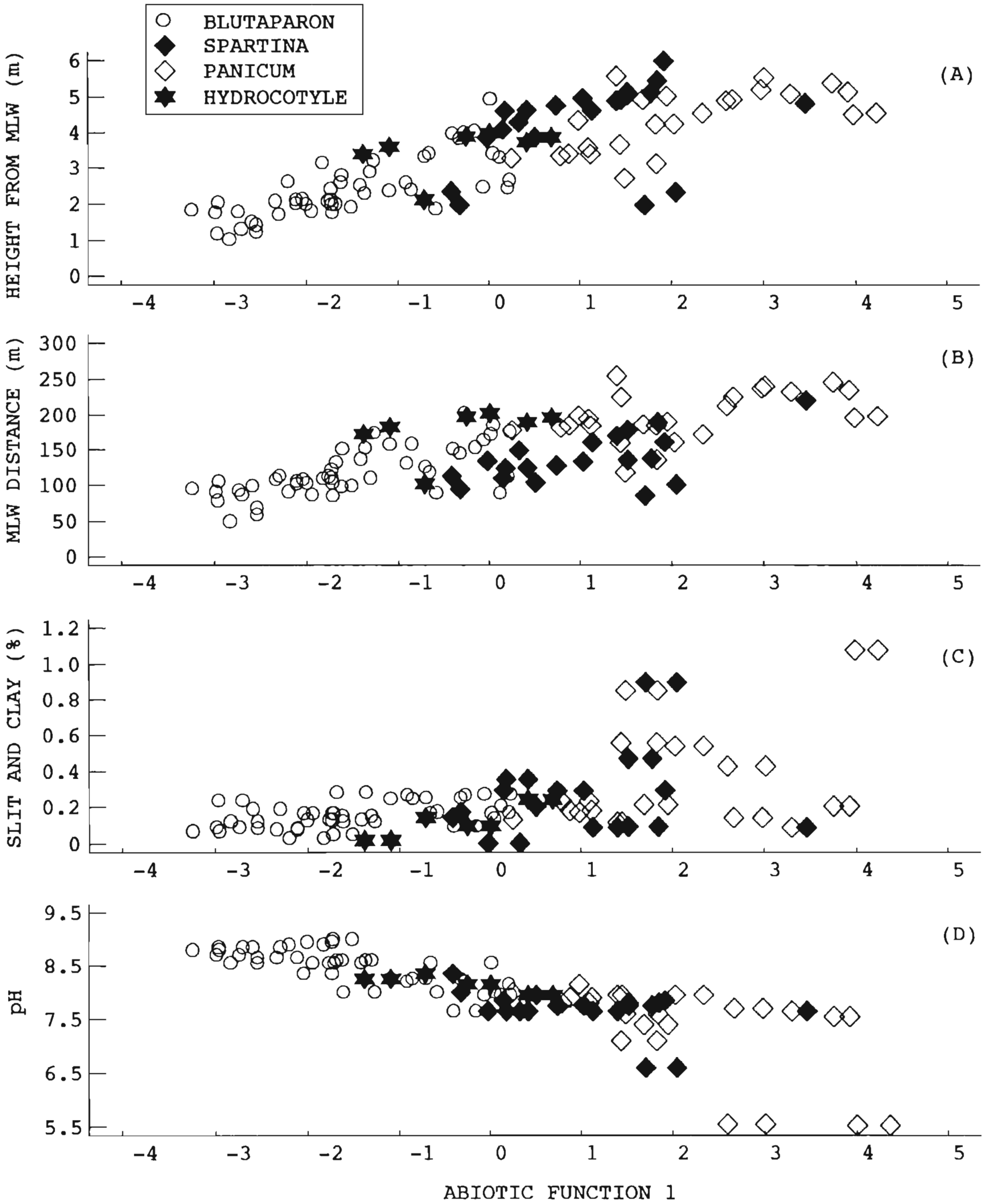

Figure 3. Relationship between the principal abiotic discriminant function and (A) dune height and (B) distance from MLW level, (C) silt and clay particles percentage and (D) pH for 100 dune zones of the southern Brazilian coast.

stitution of the *Panicum* association by a *Spartina* association; although at any given area along the coast the backshore *Blutaparon,* or occasionally the *Hydrocotyle-Paspalum* association, occur concomitantly. Northern less disturbed shores, with permanent nutrient-rich sand deposition behind the backshore favour vigorous growth of a *Panicum racemosum* association. Clonal spreading and vertical growth of the virtually monospecific *P. racemosum* stands progressively still wind-blown sand and promote up to 70 cm annual sand accreation (COSTA *et al.*, 1991). The efficient sand binding counteracts sand erosion during prevailing offshore winds and leads to formation of a prograding foredune dune ridge, which restricts the *Blutaparon* association to a narrow backshore strip. Increasing landward edaphic stability encourages invasion of *Andropogon arenarius, Conyza floribunda, Vigna luteola, Sisyrichium sp, Baccharis patens, Indigofera sabulicola, Porophyllum lanceolatum,* and *Solanum c.f. americanum* (LEGRAND, 1959; PFADENHAUER, 1980; COSTA *et al.*, 1988b; CORDAZZO and SEELIGER, 1993). Further south, gradually decreasing sand deposition and increasing seawater overwash in areas beyond the backshore leads to dominance of *Spartina* associations. Contrary to *Panicum,* a large number of highly viable seeds, rather than rhizome fragments, enable *Spartina ciliata* to rapidly occupy occasionally flooded sites close to the groundwater table (COSTA and SEELIGER, 1988b) and active salt excretion compensates for sediment salinization (BASTOS *et al.*, 1993). These conditions convey *S. ciliata* an adaptative advantage for colonization and growth at periodically disturbed humid sites. Analog substitutions (*Ammophila breviligulata* → *Spartina patens, Ammophila breviligulata* → *Panicum virgatum*) occur along the eastern coast of the United States (GODFREY, 1977; FAHRIG *et al.*, 1993). The reciprocal interaction of each plant association with allogenic factors along disturbance gradients may further our explanation into the development of different dune physiographies along time.

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